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DISTRIBUTION AND SPAWNING SITE SELECTION OF THE POLYCHAETE, *LUMBRINERIS LATREILLI* (AUDOUIN ET MILNE-EDWARDS) AT ASAMUSHI, NORTHERN JAPAN[1),2)]

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Distribution and spawning site selection of the polychaete, *Lumbrineris latreilli*, were investigated at Asamushi in northern Japan. The worms show a heterogeneous distribution even in a limited area, occurring in high density in fine sediments supporting *Zostera marina* and pebbly bottom where *Sargassum* spp. are abundant. The highest density of the adult worms is observed in the *Zostera* patches where the egg mass density is also at its highest. The worms use these sea weeds growing at, or just near, their living place for spawning. Consequently they show no marked migration to a place of suitable algal growth for spawning. The worms select their oviposition site well above the bottom surface. Experimental manipulation of the length of the algal substrates in the field showed that the selection of the spawning height is controlled by the worm's strong tendency to come up well above the bottom for oviposition. This behavior seems beneficial for successful fertilization and also for larval dispersal, since the larvae lack a swimming phase.

Polychaetes have a variety of breeding methods (see CLARK and OLIVE, 1973; SCHROEDER and HARMANS, 1975; etc.). Some groups spawn eggs in jelly masses, which are usually attached to the tubes or entrance of their burrows, on or just above the bottom. In *Diopatra variabilis,* eggs are found inside the tube held together in jelly (KRISHNAN, 1936). *Lumbrineris latreilli,* living in soft sediments, shows a unique breeding behavior. It attaches an egg mass to sea weeds but never directly to the bottom (OKUDA, 1946; NISHIHIRA *et al.*, 1980).

In the previous paper (NISHIHIRA *et al.*, 1980), we showed that *L. latreilli* had a short and definite breeding season in early June in the Asamushi area and the commencement of spawning did not correspond to a particular lunar phase but to the rise of ambient water temperature, and further the spawning occurred only at night. It was also observed that, in a limited area, both males and females

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appeared on the bottom surface, climbed the algae and released gametes simultaneously, but it remained unknown whether the worms were distributed widely over the various substrates and migrated to a spawning site of preferable algal growth, or used only those algae growing within the range of their preferred habitat, since the ecological distribution of the worms was not studied at that time. Further, they seemed to spawn almost only on algae well above the bottom, and the oviposition site on the algae was believed to be determined by the algal length and the depth of water where the algae grew. It was suspected, from the field observations, that worms ready to spawn may climb a long alga (which may reach water surface) as high as possible and spawn there.

In order to test the validity of the presented assumptions, some brief experiments and further observations were performed. In the present paper, we report and discuss the ecological distribution and spawning site selection of the worm.

Study Area and Methods

Field observations were conducted at the Marine Biological Station, Tôhoku University (MBS). At an enclosed place in the small harbor, there grow various macrophytes on the cobbly or pebbly bottoms and also on the sandy bottom, some isolated patches of *Zostera marina*. Most of the observations and experiments were made here. Some additional observations were conducted at several other sites along the shore near the MBS.

In order to study the distribution of the worms, four types of bottoms were selected in the harbor. St. 1 was set in the *Sargassum* forest on the cobbly bottom, St. 2 also in the *Sargassum* forest on the pebbly bottom, St. 3 on the level sandy bottom without any growths of macrophytes, and St. 4 in the small patches of *Zostera* growing on the sandy bottom. Four samples (each 20 cm×20 cm×10 cm) were dug out at each station. The pebbles and cobbles on the bottom were carefully removed just prior to digging at Sts. 1 and 2, and the *Zostera* above sand surface were clipped before digging at St. 4. Using the SCUBA gears, bottom samples were collected in a plastic bag by means of a knife and hands. Sampling was done in the daytime before the commencement of spawning in the area. Animals were extracted by sieving the samples with a 1 mm square mesh.

To detect migration of worms for spawning, simple modifications of the habitat (vegetation) were made and the subsequent spawning was observed. On the cobbly bottom in the harbor with good growth of macrophytes, an area of 2.7 m×2.7 m was divided into 81 small sections of 30 cm×30 cm. The central 90 cm×90 cm area (9 small sections) was cleared of macrophytes. After the completion of spawning, the egg masses in each section were counted. In another experiment, 16 thalli of *Sargassum* attached to a small stone were transplanted and arranged about 30 cm apart on the vegetation-free sandy bottom. Transplantation was also made on the *Zostera* patch, the above-ground parts of which

had been clipped. The egg masses on the algae were counted and the attachment position was recorded after the completion of spawning.

To determine the preferred spawning height, various species of *Sargassum* were sampled at both shallow and deep bottoms and the distribution of egg masses on the algae was recorded. In several patches of *Zostera*, a graded series of the length of the blades was prepared by clipping. The blades longer than the natural were artificially prepared from a vinyl tape 1 cm wide provided with a styrofoam cubic float at the tip. These were set in the cleared *Zostera* patch, and oviposition on the blades was recorded.

Results and Discussion

Distribution of Lumbrineris latreilli and egg masses

Information on the distribution of mature worms is of primary importance in discussing the distribution of egg masses. We wish to determine whether the mature worms live at the spawning site or migrate there for spawning.

Distribution of the egg masses and worms was studied in an enclosed area of the small harbor. There were many isolated patches of *Zostera marina* of various sizes on the sandy bottom, and the *Sargassum* forests on the cobbly and pebbly bottoms. After the completion of spawning in the area, the egg masses attached to the blades of *Zostera* and to the thalli of *Sargassum* were counted. Table 1 clearly shows that the egg masses are most highly concentrated in the *Zostera* patch, followed by *Sargassum* forest, but are not seen on the sandy bottom lacking sea weeds. The egg masses were a little more abundant in the *S. kjellmanianum* area than in the *S. thunbergii* area. The former area is on the cobbly bottom (shallow sublittoral) lacking large rocks, and the latter is on the cobbly bottom (lower eulittoral to shallow sublittoral) containing large rocks.

Table 1.
Mean density of egg masses of *Lumbrineris latreilli* at various sites in the enclosed small harbor of the Marine Biological Station, Tôhoku University, at Asamushi.

Vegetation	Depth (cm below ELWS)	Substrate	Egg mass density (N/m^2)
Zostera marina	120	sand	628.8
Sargassum kjellmanianum	50–100	cobble	36.9
Sargassum thunbergii	0–30	cobble	10.6
None	120	sand	0*

* A few egg masses were spawned on the transplanted *Sargassum* (see text).

The number of species and the density of animals collected at the selected stations are shown in Table 2, together with the density of *L. latreilli*. The most abundant group (both in terms of species and density) was polychaetes at all the stations. The next abundant were pelecypods, gastropods and amphipods. The

Table 2.
Number of species and individuals of the macrobenthos at 4 micro-habitats in the enclosed area in the small harbor of the Marine Biological Station, Tôhoku University, at Asamushi.

Station	St. 1		St. 2		St. 3		St. 4		Total	
Substrate Vegetation Depth (cm below ELWS)	Cobble *Sargassum* 50		Pebble *Sargassum* 100		Sand None 120		Sand *Zostera* 120			
	Spp.	No.	Spp.	No.	Spp.	No.	Spp.	No.	Spp.	No.
Nemertinea	1	1	0	-	1	1	0	-	1	2
Sipunculoidea	1	1	2	2	2	3	1	3	4	9
Polychaeta	21	150	19	72	15	70	13	284	42	579
Polyplacophora	1	1	3	5	0	-	1	1	4	7
Gastropoda	0	-	3	4	1	1	4	49	7	54
Pelecypoda	1	2	5	10	5	25	6	20	9	57
Nebaliacea	1	2	0	-	1	8	1	29	1	39
Gammaridea	5	7	3	11	1	1	2	30	5	49
Anomura	4	7	2	6	1	1	3	4	5	18
Brachyura	0	-	0	-	1	1	1	1	2	2
Cumacea	1	1	0	-	0	-	1	1	2	2
Pantopoda	0	-	0	-	0	-	1	1	1	1
Ophiuroidea	2	2	0	-	1	2	1	3	2	7
Asteroidea	1	1	0	-	0	-	0	-	1	1
Echinoidea	0	-	0	-	1	1	0	-	1	1
Total	39	175	37	113	30	114	35	426	90	828
Lumbrineris latreilli mean±SD (range)	2.00±1.63 (0-4)		0.25±2.00 (1-5)		0 -		11.75±3.86 (8-14)			

Figures are totals of 4 samples (each of 20 cm×20 cm×10 cm). At bottom of the table, mean number of *Lumbrineris latreilli* (N/0.04 m²) is shown.

similarity of species composition between sampling stations, or degree of overlap, was studied using KIMOTO's *CΠ* index (KIMOTO, 1967). If overlap is complete, the index is 1, and if there is no overlap, it is 0. The species composition was quite similar among these 4 stations as shown by the high value of KIMOTO's *CΠ*, i.e., *CΠ* value between Sts. 1 and 2 was 0.7918, that between Sts. 3 and 4 was 0.7193 and that between two pooled groups of stations, Sts. 1–2 and Sts. 3–4 was 0.6281. As to polychaetes, the species richness decreased from St. 1 to St. 4, but the density was highest at St. 4, followed by St. 1. This was due to high densities of *Lumbrineris nipponica* and *Cirriformia tentaculata* at Sts. 1 and 4, and of *L. latreilli* at St. 4. Similarity in species composition of polychaetes among the 4 stations was similar to that for all species combined. The *CΠ* value between Sts. 1 and 2 was 0.8599, that between Sts. 3 and 4 was 0.8010 and that between two combined stations, Sts. 1–2 and Sts. 3–4 was 0.6740.

Lumbrineris latreilli did not appear in the samples from the sandy bottom free from vegetation, though the sandy or muddy bottom of the area seems to be preferable for the worms, but was highly concentrated in the *Zostera* patch on the

same bottom. This suggests that the patch is a suitable habitat for this worm (at least for adults). The cobbly and pebbly bottoms supported the density only one sixth of that at the *Zostera* patch, even with good growths of *Sargassum*, the preferred substrate for oviposition (NISHIHIRA *et al.*, 1980). OKUDA (1946) reported that in Hokkaido, the adult worms of this species were found on the muddy bottom in the *Zostera*-region.

Our results show that the distribution of the adults is heterogeneous even within such a limited small area, roughly corresponding to the distribution of the egg masses. This suggests that the worms use the sea weeds within their habitat for their spawning sites, and do not migrate far for spawning. If so, it may be possible to estimate the relative density of the worms (or rather mature females) living in a place by counting the egg masses there.

Movement at spawning

The worms frequently use *Sargassum* or *Zostera* as their oviposition substrate (OKUDA, 1946, NISHIHIRA *et al.*, 1980). In general, tree-like algae with many branches were suitable. The preferability of these algae seemed not to be due to their chemical nature but rather to the morphological one, since the egg masses were seen attached to the cryptomeria branches (NISHIHIRA *et al.*, 1980) and also to the artificial *Zostera* blades (see below). As to the algal selection, however, it remains uncertain whether or not the worms actually migrate to a spawning site. Aforegoing discussion, however, suggests that the worms do not migrate for a long distance at spawning. This may be supported by the observation that many *Sargassum* carrying no egg masses were growing at certain other places, suggesting that long distance spawning migration may be infrequent, if not completely absent.

The distribution of egg masses in a small patch of the *S. thunbergii* area, the central part of which was cleared (small algae could not be removed completely), is shown in Fig. 1 a and b. The egg masses were not distributed uniformly. No egg masses were seen in the vegetation-free sections (B in b) and on the large smooth rocks, even where there was sufficient algal cover (C). Excluding these sections, the egg masses were less abundant in the cleared central part (D) than the undisturbed part (E). In the undisturbed area, the sections surrounding the cleared central part (F) supported more egg masses than the other parts (G). These tendencies were also seen in the *S. kjellmanianum* area (c). These observations suggest that the worms use the suitable algal substrates near their normal habitat. In general, the egg masses were more abundant in the *S. kjellmanianum* area than in the *S. thunbergii* area as mentioned before. The lack of spawning on the large smooth rock may be attributed to the absence of suitable crevices, which trap sediments to form the habitable situations.

In order to study the breeding migration of the worms, the thalli of

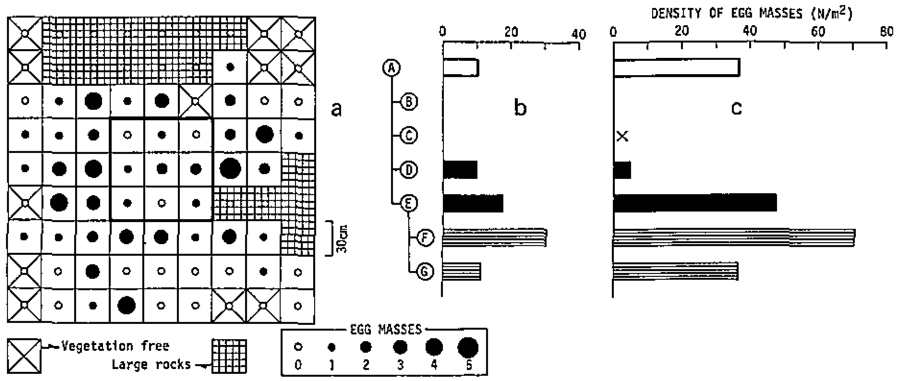

Fig. 1. Distribution of egg masses of *Lumbrineris latreilli* in the *Sargassum thunbergii* area on the cobbly bottom (a). Central 9 sections were cleared of macrophytes before the commencement of the spawning. b: Mean density of the egg masses at each type of sections for the *S. thunbergii* area. c: The same as b for the *S. kjellmanianum* area. A: Density for the whole area, B: for the vegetation-free sections, C: for the large smooth rocks, D: for the cleared central area, E: for the other vegetated cobbly area, F: for the vegetated cobbly area surrounding the cleared central area, and G: for the other vegetated area excluding D and F. X mark in c means the absence of the category C.

Sargassum were transplanted to various places and later the spawning onto them was examined. Only 4 egg masses appeared on 4 thalli out of the 16 transplanted to the vegetation-free sandy bottom. The egg mass density was $2.8/m^2$ and extremely low (comparable to the census results of the worms, Table 2). The worms which spawned there may not have migrated from adjacent *Sargassum* forest and *Zostera* patches, but may have been living there before the transplantation. Nine egg masses were found attached to the *Sargassum* (100 cm long), which was transplanted to the center of the completely clipped *Zostera* patch (25 cm$\times$30 cm). All egg masses were found on the *Sargassum* but none on the stone, *Zostera* stems and sheaths and bottom surface. The worms living in the patch may have spawned there. Based on these observations, it may be concluded that the worms spawn at the place where they are living and that they move for only a short distance, if at all, in search of suitable algal substrates.

The level of the spawning site on the algal substrates

The egg masses were concentrated around the central portion of the thalli of the longer plants of *Sargassum* growing at the intertidal or sublittoral fringe. But on the shorter algae they were mostly attached to the tip or distal portion. The formation of such a pattern was attributed to the size of algae, water depth at the time of spawning and the worm's tendency to spawn as far above the bottom as possible (NISHIHIRA *et al.*, 1980). To test this assumption, some observations and brief field experiments were conducted.

Clipping experiments of Zostera blades

The attachment positions of 38 egg masses on 28 blades in a patch of *Zostera* were studied (Fig. 2). The relative positions of the egg masses on the blades ranged from 36 to 100% with an average of 70.3% of the blade length. This shows that not all worms climbed up to the tip of the blades. This may be due to the slight curving of the blades, although the patch was situated at the sufficient depth. In other words, the tip of the intact blades is not always at the highest position from the bottom.

The distribution of egg masses on the *Zostera* blades in a patch where half of the blades were shortened by clipping is shown in Fig. 3. On 12 intact blades 14 egg masses were seen, and on 16 clipped ones there were 17 egg masses. On the intact blades, the relative position was between 43 to 89% the blade length (an average of 64.1%), which is comparable to the aforegoing result (see Fig. 2). On the clipped blades (which were about half as long as the intact ones and thus stood straight), the egg masses were found closer to the tip of the blades. The relative position showed an average of 92.0% the blade length.

In another patch, where all blades were clipped much shorter and the artificial *Zostera* was transplanted, similar results were obtained (Fig. 4). On the artificial blades, the highest position of the egg masses was 90 cm on the longest (130 cm) blade, while on the shortest one the worms spawned at the tip. The relative oviposition height on the longer blades remained at around 60% and on the shortest blade it was 100%. The longer blades intertwined due to their

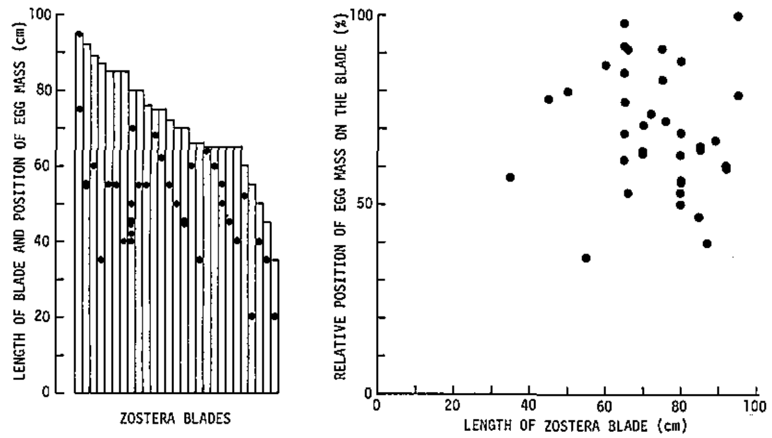

Fig. 2. Distribution of egg masses of *Lumbrineris latreilli* on the blades of *Zostera marina*. Left: Attachment positions of the egg masses (dot) on the intact blades. The length of the blade was measured from the bottom surface to the tip of the blade (each bar shows a single blade). Right: Relative positions of the egg masses on the blades plotted against the blade length. Length of the blades (mean$\pm$SD, range): 70.2$\pm$14.9, 35–95 cm; attachment position of the egg masses: 50.2$\pm$14.2, 20–95 cm; and relative position: 70.3$\pm$15.9, 36–100% of the blade length.

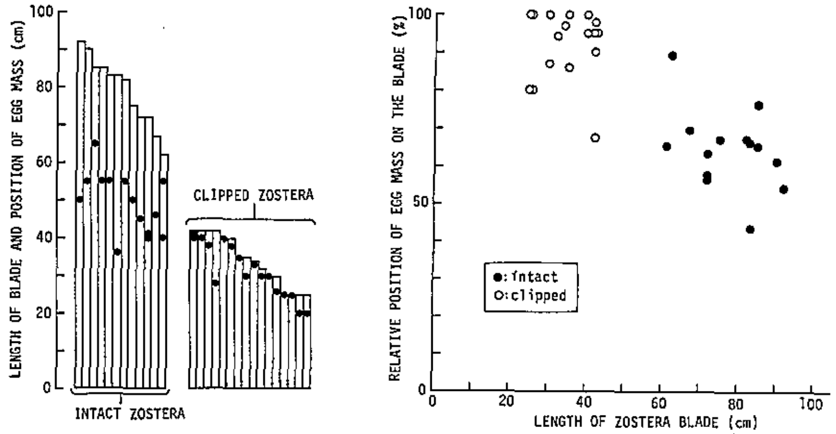

Fig. 3. Distribution of egg masses of *Lumbrineris latreilli* on the intact and clipped blades of *Zostera marina*. Left: Attachment positions of the egg masses (dot) on the intact and clipped blades in a *Zostera* patch. The length of the blade was measured from the bottom surface to the tip of the blade (each bar shows a single blade). Right: Relative positions of the egg masses on the blades plotted against the blade length. Length of the blades (mean±SD, range), intact: 79.0±9.3, 62–92 cm, clipped: 34.0±6.8, 25–42 cm; attachment position of the egg masses, intact: 49.1±8.1, 36–65 cm, clipped: 31.7±7.1, 25–42 cm; and relative position, intact: 64.1±10.7, 43–89% of the blade length, clipped: 92.0±9.3, 67–100%.

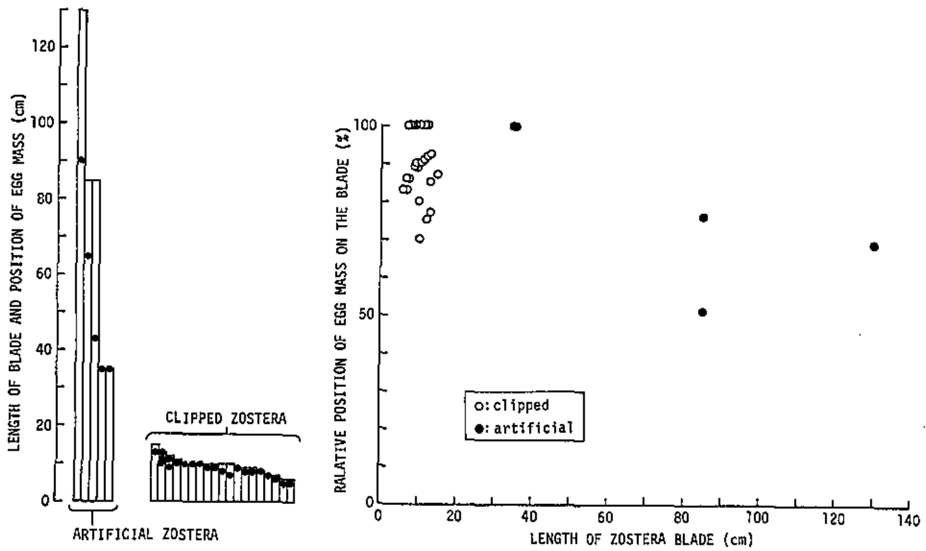

Fig. 4. Distribution of egg masses of *Lumbrineris latreilli* on the clipped blades and artificial blades of *Zostera marina*. Left: Attachment positions of the egg masses (dot) on the clipped blades and artificial blades. The length of the blade was measured from the bottom surface to the tip of the blade (each bar shows a single blade). Right: Relative positions of the egg masses on the blades plotted against the blade length. Length of the blades (mean±SD, range), artificial: 74.0±40.1, 35–130 cm, clipped: 9.6±2.3, 6–15 cm; attachment position of the egg masses, artificial: 53.6±23.8, 35–90 cm, clipped: 9.0±2.3, 5–13 cm; relative position, artificial: 79.2±21.1, 51–100 % of the blade length, clipped: 89.8±8.8, 70–100%.

flexibility while the shortest one stood straight. This may explain the observed difference in egg mass distribution. The average relative position on the artificial blades was 79.2%, which was comparable to that observed on the intact ones. The effect of clipping was remarkable. The clipped blades, standing straight, supported many egg masses whose relative positions ranged from 70 to 100% with an average of 89.8%.

These observations clearly show the strong tendency of the worm to come up well above the sea floor for oviposition if a suitable substrate is available, and further the substrate need not be a plant, since the artificial blades were also used by the worms. The worms seem not to spawn on or just above the soft bottom since no egg masses were found on the sheaths and stems of *Zostera* in the patch where all the blades were removed (see below). Instead, many egg masses were attached to the *Sargassum* transplanted to the patch.

Oviposition site on Sargassum

Assuming the worms have a tendency to come above the sea floor for spawning, the distribution of the egg masses on the *Sargassum* may vary according to the depth of the growing sites. To test this assumption some observations were made.

Many thalli of long *S. kjellmanianum* were sampled from the deep bottom in the harbor and the distribution of the egg masses was compared with that on *Sargassum* spp. growing in shallower places. On *S. hemiphyllum* growing at the sublittoral fringe, the relative attaching points ranged from 17.0 to 96.6% of the algal length with an average of 48.1% (Fig. 5 a). There was a inverse correlation between the length of algae and the relative position of the attachment height of the egg masses. This is because these egg masses were concentrated around 40 cm level, and this suggests that the worms come up to the water surface, where the longer the algal thallus, the longer the part of alga being bent and floating horizontally at the water surface (Nishihira *et al.*, 1980). On *S. thunbergii* growing in the lower eulittoral to sublittoral fringe, the average attachment height was 35.3 cm and the relative positions ranged from 28.6 to 100% with an average of 74.1% (Fig. 5 b). The actual attachment height was not different significantly from that on *S. hemiphyllum* but the relative position was higher in *S. thunbergii*. This is due to the relatively shorter algal thalli in the latter species. However, on *S. kjellmanianum* sampled at the deeper place, the average attachment height was 58.9 cm and the relative positions ranged from 48 to 100% with an average of 86.3% (Fig. 5 c). These figures are higher than those on the aforegoing two species. *S. kjellmanianum*, growing in the deeper bottom, stood straight even at low tides.

The oviposition height on the main branches of a *Sargassum* (135 cm long) growing at the deeper place and consequently standing straight at low tides was examined (Fig. 6 a). The length of the main branch is represented by the length from the holdfast to the tip of the branch. The egg masses were concentrated in

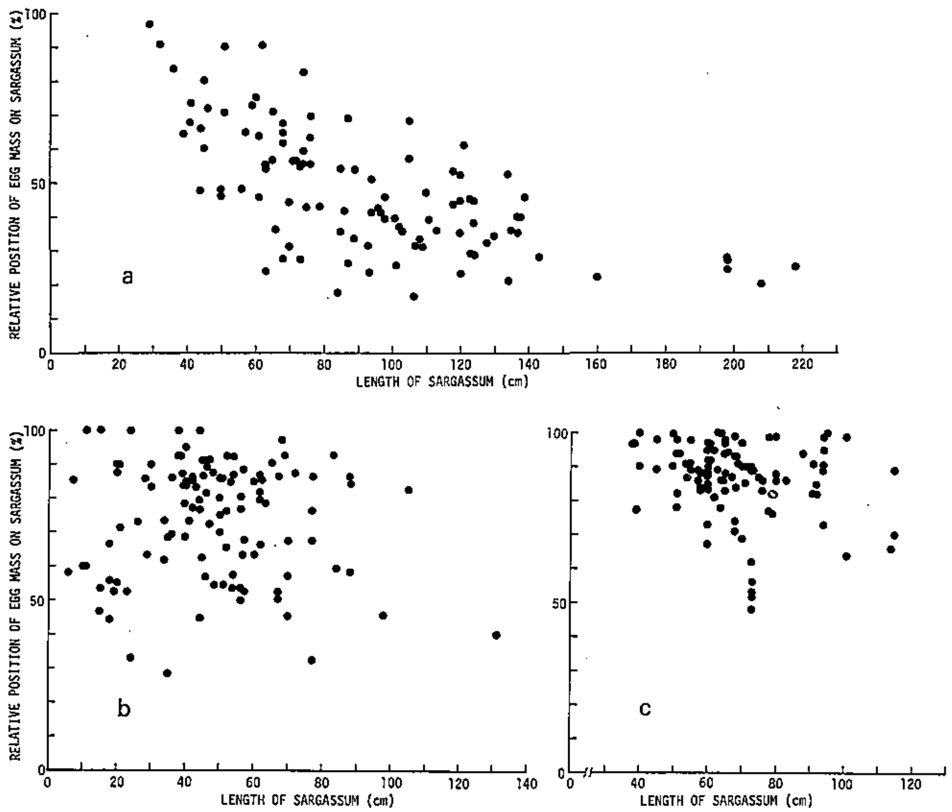

Fig. 5. Relative attachment positions of egg masses of *Lumbrineris latreilli* on *Sargassum* spp. plotted against the length of *Sargassum*. The length of *Sargassum* was measured from the holdfast to the tip of the thallus. a: *Sargassum hemiphyllum* growing at sublittoral fringe, b: *S. thunbergii* growing at lower eulittoral zone to sublittoral fringe, and c: *S. kjellmanianum* growing at sublittoral zone, 120 cm below ELWS, thus standing straight at low tides. Length of the algae (mean±SD, range), a: 89.8±38.4, 29–218 cm, b: 46.9±22.4, 6–131 cm, c: 66.4±16.7, 38–115 cm; attachment position of the egg masses, a: 40.2±12.8, 15–74 cm, b: 35.3±16.9, 3.5–87 cm, c: 58.9±14.8, 30–102 cm; relative position of the egg masses, a: 48.1±18.3, 17.0–96.6% of the algal length, b: 74.1±16.9, 28.6–100%, c: 86.3±11.1, 48–100%.

the upper portion of the main branches, and the relative positions ranged from 67 to 99% with an average of 85.6%. The attachment position of the egg masses on the main branches of a *Sargassum* (100 cm long) transplanted to the patch of *Zostera* where all the *Zostera* were removed by clipping was measured (Fig. 6 b). The depth of this patch was 120 cm below ELWS. Most of the egg masses were concentrated above 90% length of branch, the average relative position being 91.5%. No egg masses were attached to the clipped *Zostera* stems and sheaths. This suggests that if the longer substrates are available, the worms select them, while the potentially suitable substrates (*Zostera*) situated just near the bottom surface are not used. Similarly, on the *Sargassum* set on the vegetation-free sandy bottom

near the *Zostera* patch, the relative position was high showing an average of 88.5 %.

These observations also show that the worms select their oviposition sites as high as possible. The worms crawl on the algal surface to come up to the oviposition sites (NISHIHIRA *et al.*, 1980), and do not swim freely to the water surface.

Water movement seems to be stronger near the water surface than at the bottom, so that the dispersal of the sperm, which are laid in a cluster on sea weeds and disperse due to water movement (NISHIHIRA *et al.*, 1980), and consequently the chance of fertilization may also be greater near the water surface. The distance between the egg masses and the bottom may be important for the dispersal of the larvae which lack a free-swimming phase. If the egg mass is attached directly to the bottom, the larval recruitment may concentrate within a very limited area around the egg mass, even if they develop normally. The dispersal of the larvae is passive, being dependent on the water movement. Therefore, the larvae from those egg masses deposited well above the bottom may disperse well. Those species that attach egg masses to the algal substrates generally produce non-pelagic larvae. OKUDA (1946) said that *Neanthes* sp. laid eggs in clusters embedded together in jelly mass protected by the tough, more or less elastic white silky envelope, and such egg masses were abundantly found attached firmly to the leaves of *Zostera* at Akkeshi, Hokkaido, and these larvae lacked the free-swimming stage. Our *L. latreilli* also lacks the free-swimming stage. Although some species which attach egg masses to the bottom or their tubes have

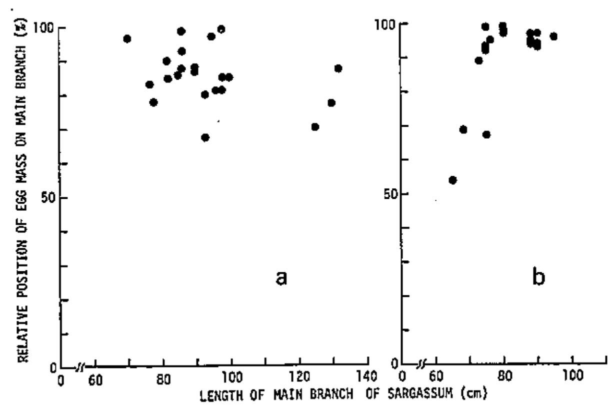

Fig. 6. Relative positions of egg masses of *Lumbrineris latreilli* on the main branches of a *Sargassum kjellmanianum* growing on the deep bottom (a), and on those of another thallus (same species) transplanted to the patch of *Zostera marina* (all the blades of which being clipped) (b). Both *Sargassum* stood straight at low tides. Length of the main branches was measured from the holdfast to the tip of the branch. Length of the main branches (mean±SD, range), a: 95.6±18.0, 70–132 cm, b: 77.9±8.9, 65–95 cm; attachment position of the egg masses, a: 79.8±12.4, 61–115 cm, b: 73.2±15.3, 35–91 cm; relative position, a: 85.6±8.5, 67–99% of the length of main branch, b: 91.5±11.8, 54–99%.

pelagic larvae, others do not. According to OKUDA (1946), FEWKES (1883) reported that *Lumbriconereis* (=*Lumbrineris*) sp., giving no specific name, attached egg masses to the mud and that the larvae lacked a free-swimming phase.

Consequently, it is not proven that the worms come up to the algae because it is beneficial for the larval dispersal. Nevertheless, attaching egg masses to the algal substrates well above the bottom should have some meaning in their life history. More investigations are required for better explanation of such behavior.

The breeding behavior of *L. latreilli* may expose individuals to predators at 3 stages, 1) when the adults move to the spawning site, 2) while the egg masses are left unprotected at the spawning site, and 3) when the larvae are dispersed by water movement. The benefits of spawning as high as possible must be very great to outweigh the danger of predation, or else *L. latreilli* must have some powerful protective mechanism(s). This is a matter for further investigation.

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